Dive depth and plumage air in wettable birds: the extraordinary case of the imperial cormorant

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ABSTRACT: Cormorants are considered to be remarkably efficient divers and hunters. In part, this is due to their wettable plumage with little associated air, which allows them to dive with fewer energetic costs associated with buoyancy from air in the feathers. The literature attributes particularly exceptional diving capabilities to cormorants of the 'blue-eyed' taxon. We studied the diving behaviour of 14 male imperial cormorants *Phalacrocorax atriceps* (included in the blue-eyed taxon) in Patagonia, Argentina, and found that this species did indeed dive deeper, and for longer, than most other non-blue-eyed cormorant species. This species also exhibited longer dive durations for any depth as well as longer recovery periods at the surface for particular dive durations. We propose that this, coupled with atypically long foraging durations at sea in cold water, suggests that cormorants of the blue-eyed complex have a plumage with a substantial layer of insulating air. This is given credence by a simple model. High volumes of plumage air lead to unusually high power requirements during foraging in shallow, warmer waters, which are conditions that tend to favour wettable plumage. However, deep dives and/or cold water should favour the blue-eyed phenotype, which explains their essentially high latitude distribution.

KEY WORDS: Diving behaviour · Cormorants · Patagonia · Argentina · Buoyancy · Insulation

INTRODUCTION

Cormorants are cosmopolitan fish-eating aquatic predators and members of the 39 species that comprise the genus *Phalacrocorax* (Orta 1992). They frequent both coastal and inland waters from polar to tropical regions, breeding in colonies numbering from just a few individuals to many thousands of birds (Johnsgard 1993). The obvious success of this group has been attributed to their efficiency as aquatic predators (Gremillet et al. 2001, 2005a), this being related to their swimming and diving abilities (Gremillet 1997, Gremillet et al. 2004) that are, in part, a result of their wettable plumage (Ribak et al. 2005, Gremillet et al. 2005b), which results in reduced buoyancy. Despite this, cormorants are often cited as diving shallowly, primarily exploiting the first 10 m of the water

column in dives that rarely exceed 1 min (for review see Cooper 1986). A notable exception to this appears to be the blue-eyed, Southern Ocean cormorants (also called shags), which consist of 13 taxa (Orta 1992). To date, aspects of the diving behavior of blue-eyed cormorants have been described for birds mainly from sub-Antarctic colonies using data derived from radiotelemetry (Wanless et al. 1992, Sapoznikow & Quintana 2003) and time-depth recorders (Croxall et al. 1991, Kato et al. 1996, 2000, Wanless et al. 1999, Tremblay et al. 2005). These data indicate that blue-eyed cormorants are indeed exceptional divers, their current maximum recorded depth being 145 m (Tremblay et al. 2005) and maximum duration being 380 s (Wanless et al. 1992).

Given that blue-eyed cormorants appear morphologically very similar to other members of the genus, it is

not immediately obvious why their apparent diving ability should be greater than that of congeners. In this study, we documented the diving behavior of 14 male imperial cormorants *Phalacrocorax atriceps* breeding in Patagonia, Argentina, using time-depth recorders. We examined these and other published data on dive performance by members of the Phalacrocoracidae to examine the extent to which these birds really are exceptional among cormorants, and attempted to explain the patterns observed. For this, we used standard simple models describing how plumage air thickness varies with depth (cf. Wilson et al. 1992, Gremillet et al. 1998b), and how this relates against buoyancy and energy lost as heat. We noted that aspects of our data set were previously published (Wilson & Quintana 2004) in a discussion of other matters not directly relevant to this work.

MATERIALS AND METHODS

Fieldwork was conducted at 2 sites in coastal Chubut, Argentina: Caleta Malaspina (45° 11′ S, 66° 30′ W) between 3 and 20 December 2001, and Punta León (43° 04′ S, 64° 2′ W) between 1 and 4 December 2003. The former is an inlet of 34 km^2, with a maximum width of 4 km and length of 10 km. The imperial cormorants breed at 2 islands: Vernaci Este (VE) at the mouth of the inlet, and Vernacci Oeste (VO) inside the inlet, separated by 2.2 km. Yorio et al. (1998) reported 375 and 298 pairs of imperial cormorants breeding at VE and VO, respectively. At Punta León, a silt platform of approximately 5 ha lying seaward of the 100 m tall cliffs provides nesting habitat for several seabird species, including approximately 3050 imperial cormorant pairs (Yorio et al. 1998).

Time-depth recorders (TDR Mk7, Wildlife Computers) were deployed on 15 adult male imperial cormorants (7 at VE and 8 at VO) during the first 10 d of the chick-rearing period. Male imperial cormorants were sexed by vocalizations (males 'honk' and females 'hiss', see Malacalza & Hall 1988). The TDRs measured $10 \times 2 \times 1$ cm and weighed 30 g, less than 1.5% of adult body mass (mean: 2400 g; range: 2200 to 2500 g). Devices were attached to the feathers using waterproof tape and 2 cable-ties in the centre/lower back to minimize hydrodynamic drag (Bannasch et al. 1994). The procedure was completed in less than 5 min and birds quickly returned to their nest. All birds carrying devices continued to breed normally during the study period. Depth data were recorded with a resolution of 0.5 m at 1 Hz. Birds were recaptured after several foraging trips (1 to 10, undertaken during periods of between 1 and 5 d), the TDRs removed and the data downloaded.

Four birds, 1 female and 3 males, were equipped with other TDRs (high resolution DK 16-D series, Driesen and Kern) at Punta León. The devices were attached in the same way as those of Wildlife Computers and recovered (when possible) after a single foraging trip. The units recorded depth with a resolution better than 1 cm at a frequency of 10 Hz. These units were deployed specifically to determine stroking frequency as a function of depth, in order to estimate the potential effect that buoyancy might have on the foraging ecology of this species.

Data obtained from the Wildlife Computer TDRs were analyzed using the programme MTDIVE (Jensen Software Systems). This programme graphically displays depth data against time, and then places cursors at the start and end of dives as well as at points of inflection in the dive profile to indicate the initiation and end of the bottom phase when birds forage along the seabed. The appropriateness of the cursor positions was checked visually before data were written to an ASCII spreadsheet, with the following parameters for each dive being determined: time of initiation of each dive, duration and rate of the descent, bottom and ascent phases, and maximum depths reached during the dive. Pelagic dives were defined as V-shaped dives, with bottom durations of less than or equal to 2 s (twice the recording interval of the TDRs), whereas benthic dives were defined as U-shaped dives, with bottom durations of at least 3 s.

Differences among individuals with regard to diving (e.g. depth, dive duration, surface duration etc.) were tested using a Kruskal-Wallis test or 1-way ANOVA, depending on normality. In all cases, differences among individuals were significant to at least the p < 0.05 level or better. Mean values for all parameters were determined for each bird and then pooled to calculate overall mean (±SD).

Depth data recorded by the high resolution DK 16D devices were analyzed using the program MT-WIN (Jensen Software Systems). This programme displays data in much the same way as MTDIVE (see above), but the data can be assessed so as to derive rates of change in depth ($\Delta D/\Delta t$, where t is time) in order to look for periods of acceleration and deceleration corresponding to kicks used in swimming.

RESULTS

All TDRs deployed were successfully recovered from the 15 birds equipped at Caleta Malaspina. However, 1 instrument failed, and data could not be downloaded for 1 of 8 cormorants from VO. The maximum deployment period was 9 d, during which diving activity could be recorded for up to 5 d before the memory was

full. No instrumented birds lost chicks during the study period. A data set of 56 bird-days at sea was obtained, consisting of almost 240 h of diving activity that represented 2993 dives distributed over 91 foraging trips of the 14 cormorants (Table 1).

Birds generally performed between 1 and 2 foraging trips per day. Mean number of dives per day was 54.3 ± 29.7 (n = 26 d, 14 birds). The maximum number of dives per day was 126. However, days with more than 100 dives were infrequent and constituted less than 8% of the data. The cormorants were almost exclusively diurnal feeders, foraging from dawn to dusk. However, most dives (84%) were initiated after 13:00 h. Almost 50% of dives were made after 18:00 h and diving activity lasted until a maximum of 52 min after sunset (21:10 h).

Imperial cormorants foraged over a wide range of depths. Although maximum dive depth was bimodally distributed with modes around 5 to 10 m and 25 to 30 m, over 50% of all dives were directed to depths in

Table 1. *Phalacrocorax atriceps.* Summary statistics from diving records of 14 male imperial cormorants breeding at Patagonia, Argentina. Data are mean ± SD (max.)

Bird	No. of dives	Maximum depth (m)		Dive duration (s)		Surface interval (s)		Bottom duration (s)		Bottom time (%)
Vernaci Este (VE)										
1	243	35.1 ± 13.1	(57.5)	105.6 ± 43.5	(198)	182.6 ± 168.8		54.8 ± 31.9	(125)	47.6 ± 18.0
2	449	24.9 ± 8.9	(47.0)	92.3 ± 32.1	(185)	102.5 ± 122.6		57.0 ± 28.3	(174)	58.2 ± 19.7
3	180	32.9 ± 22.9	(68.7)	118.0 ± 66.8	(280)	248.0 ± 212.0		69.6 ± 45.0	(267)	57.0 ± 19.6
4	131	25.9 ± 6.9	(33.5)	97.9 ± 25.3	(136)	126.3 ± 73.1		59.0 ± 20.4	(92)	58.3 ± 12.9
5	141	25.9 ± 11.0	(52.5)	115.9 ± 45.8	(212)	183.2 ± 132.2		78.5 ± 34.9	(144)	65.7 ± 14.4
6	182	32.4 ± 11.4	(56.5)	119.3 ± 35.5	(187)	189.2 ± 122.6		72.2 ± 26.0	(117)	59.0 ± 16.3
7	153	31.0 ± 10.8	(57.7)	120.0 ± 37.7	(205)	210.5 ± 122.3		72.3 ± 28.5	(133)	58.4 ± 14.2
Mean ± SD		**29.7 ± 4.1**		**109.9 ± 11.3**		**177.5 ± 49.2**		**66.2 ± 9.2**		**57.7 ± 5.3**
Vernaci Oeste (VO)										
1	364	15.0 ± 12.9	(47.0)	60.1 ± 36.0	(166)	99.8 ± 127.0		36.0 ± 23.3	(113)	57.1 ± 18.2
2	214	39.1 ± 14.2	(58.5)	129.5 ± 47.8	(197)	232.3 ± 145.7		74.8 ± 35.4	(132)	53.5 ± 17.3
3	202	34.8 ± 13.9	(59.5)	108.8 ± 39.5	(197)	184.8 ± 147.2		62.9 ± 26.5	(118)	56.9 ± 15.1
4	60	23.2 ± 14.5	(48.0)	82.8 ± 51.1	(193)	161.7 ± 185.8		47.0 ± 33.2	(107)	53.3 ± 14.7
6	399	10.4 ± 11.0	(49.5)	55.7 ± 31.4	(156)	51.1 ± 88.8		39.0 ± 18.6	(95)	73.1 ± 22.7
7	176	30.7 ± 8.5	(60.0)	93.5 ± 21.4	(168)	125.4 ± 138.0		48.1 ± 15.5	(93)	50.4 ± 12.2
8	99	29.5 ± 17.7	(69.0)	105.6 ± 47.2	(191)	185.2 ± 181.6		64.5 ± 27.1	(108)	62.9 ± 18.3
Mean ± SD		**26.1 ± 10.4**		**90.9 ± 26.7**		**148.6 ± 60.9**		**53.2 ± 14.4**		**58.2 ± 7.7**
Total	**2993**									
Total Mean ± SD		**27.9 ± 7.9**		**106.4 ± 4.0[a]**		**177.6 ± 43.2[a]**		**59.7 ± 13.4**		**60.0 ± 6.3**

[a]Birds 1 and 6 from VO excluded owing to short immersion time

Bird	Descent time (s)		Ascent time (s)		Descent rate (m s^{-1})		Ascent rate (m s^{-1})	
Vernaci Este (VE)								
1	25.6 ± 8.7	(50)	25.2 ± 10.1	(85)	1.3 ± 0.2	(1.5)	1.3 ± 0.2	(1.6)
2	18.4 ± 7.4	(87)	16.9 ± 11.6	(166)	1.2 ± 0.3	(3.7)	1.5 ± 0.5	(5.2)
3	24.8 ± 15.2	(51)	23.6 ± 16.5	(94)	1.1 ± 0.3	(1.5)	1.3 ± 0.3	(2.3)
4	19.4 ± 4.7	(27)	19.5 ± 5.6	(35)	1.2 ± 0.2	(1.3)	1.2 ± 0.2	(1.6)
5	20.5 ± 7.9	(44)	16.9 ± 7.0	(38)	1.1 ± 0.2	(1.4)	1.4 ± 0.3	(2.5)
6	23.4 ± 9.7	(95)	23.8 ± 9.2	(49)	1.2 ± 0.2	(1.8)	1.3 ± 0.6	(7.5)
7	24.5 ± 7.8	(51)	23.1 ± 8.6	(53)	1.2 ± 0.1	(1.4)	1.3 ± 0.2	(1.7)
Mean ± SD	**22.4 ± 2.9**		**21.3 ± 3.5**		**1.2 ± 0.06**		**1.3 ± 0.1**	
Vernaci Oeste (VO)								
1	12.9 ± 8.1	(34)	11.2 ± 8.2	(49)	1.0 ± 0.3	(1.7)	1.2 ± 0.4	(2.0)
2	27.4 ± 8.9	(40)	27.3 ± 9.8	(67)	1.3 ± 0.2	(1.6)	1.3 ± 0.2	(1.8)
3	23.2 ± 9.0	(38)	22.7 ± 10.4	(50)	1.4 ± 0.1	(2.1)	1.5 ± 0.3	(4.5)
4	19.0 ± 11.3	(53)	17.6 ± 10.3	(40)	1.0 ± 0.4	(2.5)	1.0 ± 0.3	(1.9)
6	8.1 ± 9.2	(42)	8.6 ± 9.6	(48)	1.3 ± 0.3	(4.0)	1.2 ± 0.5	(7.7)
7	23.8 ± 6.0	(42)	21.6 ± 6.5	(48)	1.1 ± 0.1	(1.9)	1.3 ± 0.2	(2.0)
8	20.9 ± 12.9	(51)	20.2 ± 14.2	(56)	1.2 ± 0.2	(1.5)	1.4 ± 0.4	(4.0)
Mean ± SD	**19.3 ± 6.7**		**18.5 ± 6.6**		**1.2 ± 0.2**		**1.3 ± 0.2**	
Total Mean ± SD	**20.8 ± 5.2**		**19.9 ± 5.3**		**1.2 ± 0.1**		**1.3 ± 0.1**	

excess of 28 m (Fig. 1A). Mean maximum dive depths of birds were similar between colonies (Mann-Whitney U-test, $Z = 0.7$). Mean maximum dive depth was 27.9 m (SD 7.9, n = 14 birds, 2993 dives). The maximum depth recorded for any bird was 69 m (Table 1). Maximum depth reached during a dive was highly and positively correlated with total dive duration, according to a linear function where:

duration = $26.2 + 2.6D$ ($r^2 = 0.77$, p < 0.05) (Fig. 2A)

where D is depth (m). Mean dive duration was 106 s (SD 4 s, n = 12 birds), but all cormorants executed some dives that lasted more than 120 s, with over 50% of all dives exceeding 100 s (Fig. 1B). Maximum dive duration recorded was 280 s (Table 1). Mean time at the surface between successive dives (surface duration), excluding prolonged surface intervals (i.e. those in excess of 15 min [900 s, which constituted only 2% of total surface intervals]), was 178 s (see Table 1). Despite considerable variance, there was a clear relationship between the time taken at the surface between

dives and the maximum dive depth reached in the preceding dive, with the relationship being best described by:

surface pause duration = $19.5e^{0.05D}$ ($r^2 = 0.58$, p < 0.0001) (Fig. 2B)

During dives, the duration of the descent was slightly greater than that of the ascent phase (20.8 ± 5.2 vs. 19.9 ± 5.3 s) (Wilcoxon matched pairs test, $Z = 2.5$, p < 0.05, n = 14 birds) (Table 1). Both diving variables were related to maximum dive depth according to linear regressions:

descent duration = $2.5 + 0.65D$ ($r^2 = 0.89$, p < 0.05)

and

ascent duration = $1.7 + 0.65D$ ($r^2 = 0.68$, p < 0.05)

Vertical velocities for descent and ascent (measured as rates of change in depth during the descent and ascent phases) were independent of depth during any single descent/ascent (cf. Fig. 3) and were 1.2 ± 0.1 and 1.3 ± 0.1 m s^{-1}, respectively (n = 7 birds per colony) and were poorly correlated with the maximum depth of dives (r = 0.3 and 0.2 for descent and ascent velocities, respectively, p < 0.05).

During 95% of dives, the cormorants spent extended time at a particular maximum depth, giving a U-shaped dive profile (see 'Materials and methods'). In 5% of dives, and in all individuals, birds dived to a specific depth before returning virtually immediately to the surface (V-shaped). Maximum dive depth, dive duration, descent and ascent vertical velocities were significantly lower for V-dives than for U-dives (Mann-Whitney U-test, $Z = 9.0$, 14.4, 13.6 and 15.5, respectively p < 0.01).

Mean bottom duration was almost 1 min (59.7 ± 13.4 s, n = 14 birds). The maximum duration spent foraging at the seabed during any one dive was 267 s, and all birds performed dives where they spent in excess of 91 s at the bottom. There was a positive relationship between the amount of time spent at the point of maximum depth in U-shaped dives (bottom duration) and maximum dive depth, according to:

bottom duration = $25.9 + 1.25D$ ($r^2 = 0.38$, p < 0.0001)

Of the 4 birds equipped with high resolution depth loggers (DK 16) at Punta León, 1 malfunctioned due to water ingress. The memory of 2 others was full before systematic,
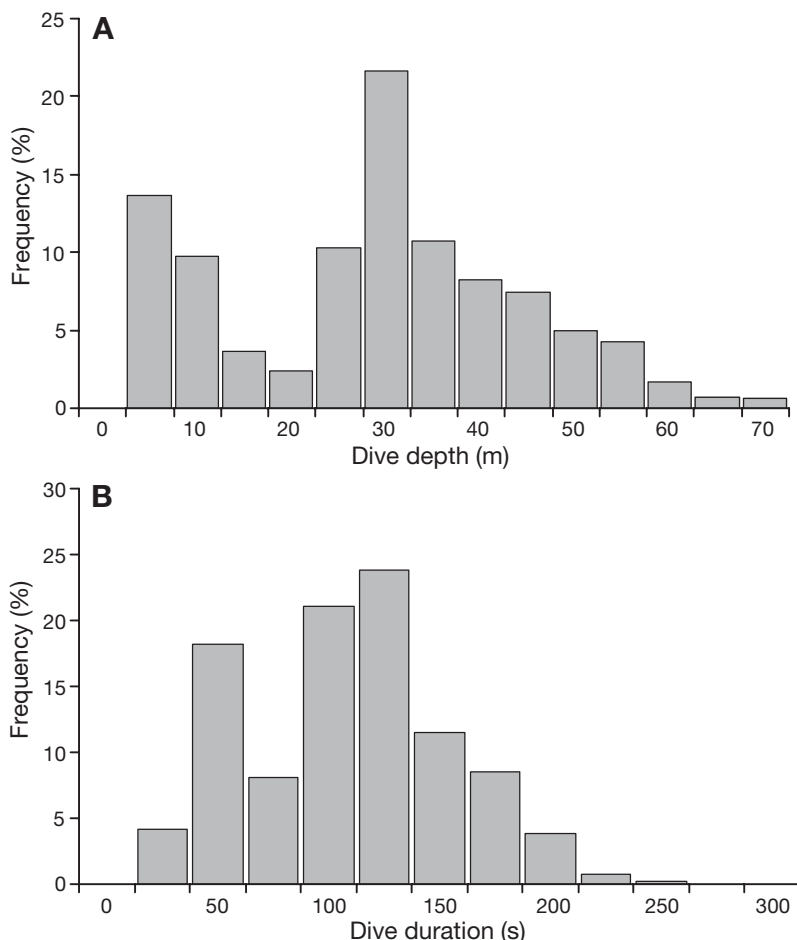

Fig. 1. *Phalacrocorax atriceps.* Frequency distribution of (A) maximum dive depths and (B) maximum dive duration of imperial cormorants foraging over the Patagonian Shelf, Argentina (n = 14 birds, n = 2293 dives)

deep diving was undertaken, so that these devices only recorded short shallow dives to a maximum of 9 m (which appeared to be largely exploratory, rather than foraging, dives). However, 1 unit recorded all dives for a full foraging period of 365 min. Relationships between total dive duration, descent duration, bottom duration, ascent duration, and maximum depth reached during dives were within the 95% confidence limits of the birds from Caleta Malaspina. This unit showed systematic variation in the descent rate (Fig. 3A), which we interpreted as being due to the foot kicks used in propulsion. These kicks were most apparent during the descent (Fig. 3A), where they decreased in frequency with increasing depth (Fig. 3B).

DISCUSSION

Our results show that imperial cormorants routinely dive to depths in excess of 20 m and for longer than 100 s (Fig. 1), which appears excessive for cormorants in general (Cooper 1986). However, if species-specific maxima are considered, our results, together with others previously published, indicate that members of the blue-eyed cormorant complex dive both deeper

(Fig. 4A; $t = 4.25$, $p < 0.005$) and longer (Fig. 4B; $t = 7.24$, $p < 0.001$) than other cormorant species. Species mass is indicated in the figures because the effects of allometry are considered important in dive capacities (Schreer & Kovacs 1997, Schreer et al. 2001). We note however that phylogenetic information should ideally be included (Halsey et al. 2006), something that we did
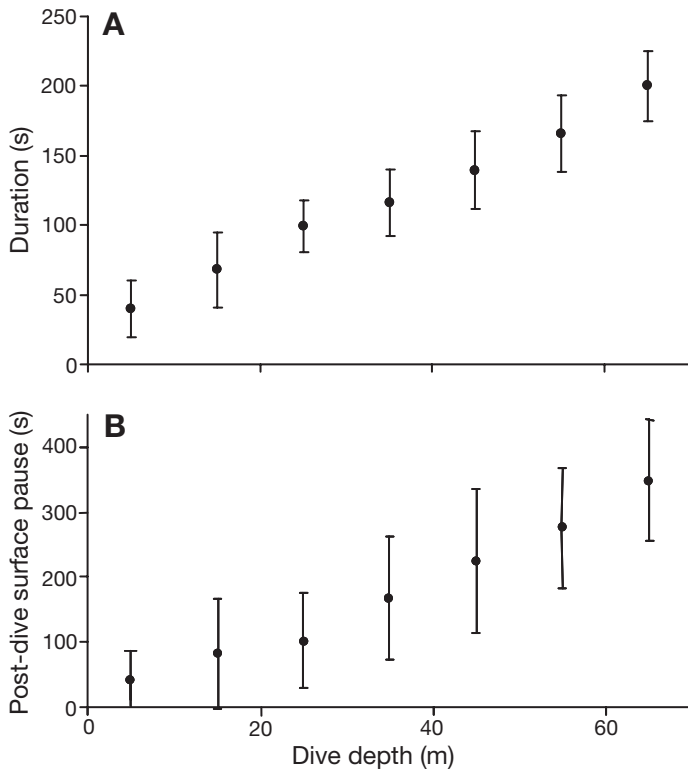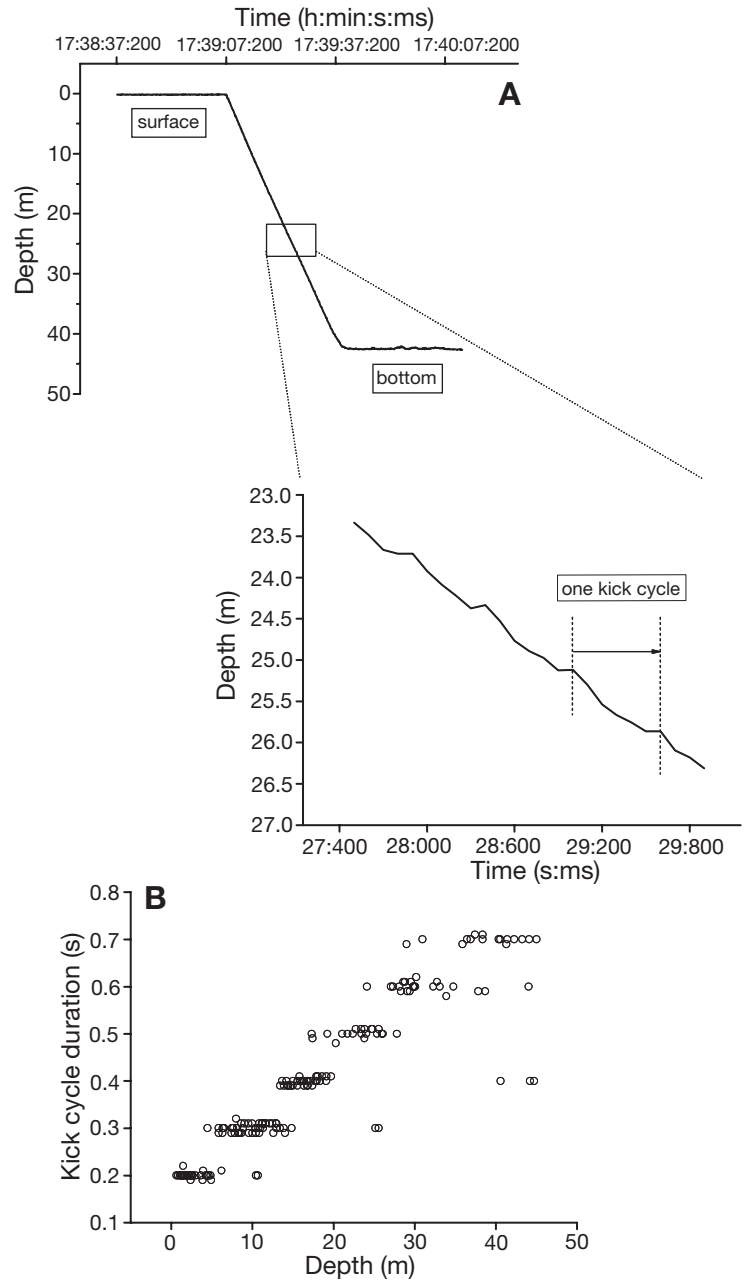

Fig. 3. *Phalacrocorax atriceps.* (A) Section of the descent and bottom phase of a dive (depth vs. time) made by an imperial cormorant to 43 m, with an enlarged inset of ~25 m depth to show systematic variation attributed to kicks used in descent. (B) Relationship between kick cycle duration and depth in the same bird during a series of 13 dives, all executed to a maximum depth of 46 m

Fig. 2. *Phalacrocorax atriceps.* Relationship between (A) total dive duration and (B) post-dive surface pause duration and maximum dive depth for imperial cormorants foraging over the Patagonian Shelf, Argentina (n = 14 birds, n = 2293 dives). Data are mean per depth class ± SD
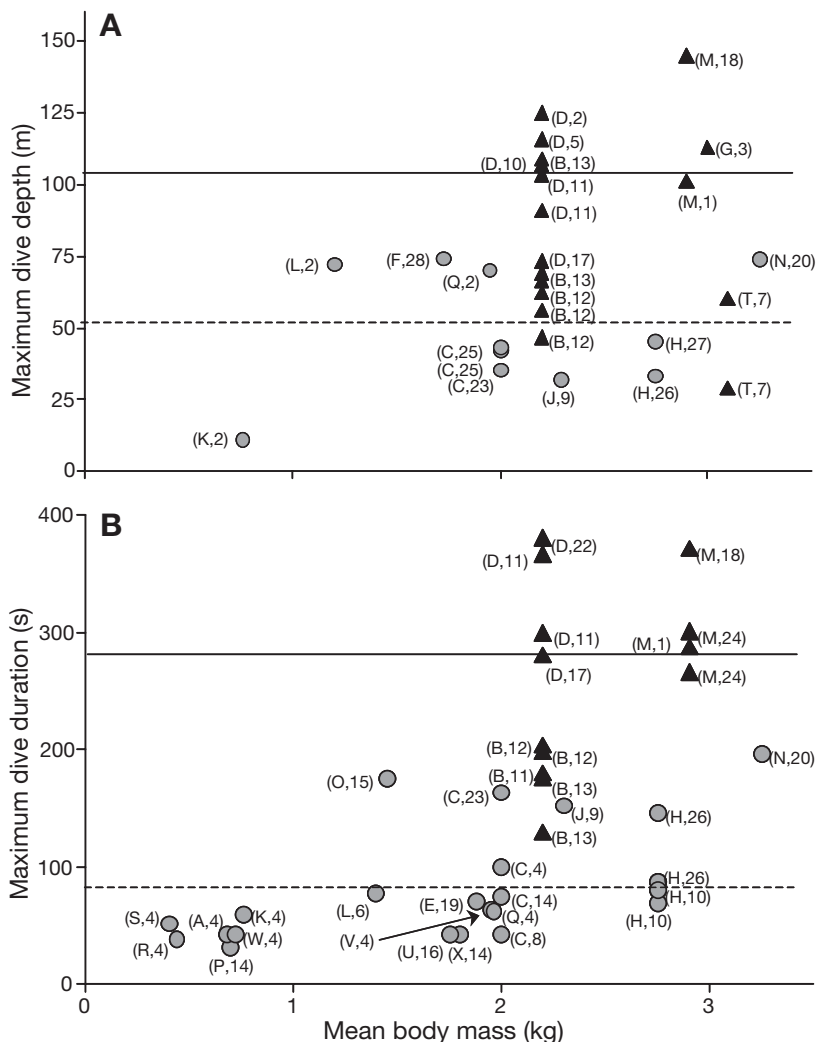
Fig. 4. Mean maximum (A) dive depth and (B) dive duration of various cormorant species. Horizontal lines are blue-eyed cormorant mean (solid line) and non-blue-eyed cormorant mean (dashed line); all values calculated from species (rather than study site) maxima. Depths derived only from records of depth gauges attached to birds: records from nets are equivocal because birds can be caught while the net is being lowered. Where depth values from the literature were only given as mean ± SD, maxima were approximated by mean + 2 SD. Durations were derived from depth gauges, VHF telemetry or visual observation. Masses are medians from Orta (1992) or unpubl. data. ▲: blue-eyed cormorants; ●: non-blue-eyed cormorants; A, *Phalacrocorax africanus*; B, *P. albiventer*; C, *P. aristotelis*; D, *P. atriceps*; E, *P. auritus*; F, *P. bougainvillii*; G, *P. bransfeldensis*; H, *P. capillatus*; I, *P. capensis*; J, *P. carbo*; K, *P. coronatus*; L, *P. gaimardi*; M, *P. melanogenis*; N, *P. harrisi*; O, *P. magellanicus*; P, *P. melanoleucas*; Q, *P. neglectus*; R, *P. niger*; S, *P. nigrogularis*; T, *P. nivalis*; U, *P. olivaceous*; V, *P. pelagicus*; W, *P. pygmeus*; X, *P. varius*. Numbers refer to source data: 1, Bevan et al. (1997); 2, Burger (1991); 3, Casaux et al. (2001); 4, Cooper (1986); 5, Croxall et al. (1991); 6, Frere et al. (2002); 7, Green & Williams (1997); 8, Gremillet et al. (1998a); 9, Gremillet & Wilson (1999); 10, Ishikawa & Watnuki (2002); 11, Kato et al. (1992); 12, Kato et al. (1996); 13, Kato et al. (2000); 14, Lea et al. (1996); 15, Quintana (1999); 16, Quintana et al. (2004); 17, this study; 18, Tremblay et al. (2005); 19, data from http://www.inhs.uiuc.edu/chf/pub/ifwis/birds/double-crested-cormorant.html; 20, H. Vargas (unpubl. data); 21, Wanless & Harris (1991); 22, Wanless et al. (1992); 23, Wanless et al. (1993); 24, Wanless et al. (1995); 25, Wanless et al. (1999); 26, Watanuki et al. (1996); 27, Wilson & Wilson (1988); 28, Zabalaga & Paredes (1999). Doubled species with authors refer to inter-sex or inter-locality differences. Arrow indicates data point V, 4

not attempt owing to uncertainties in cormorant phylogeny (Orta 1992). Although the birds we equipped did not achieve depths or durations equivalent to some of the sub-Antarctic imperial cormorants, they were apparently precluded from diving deeper because they were foraging over the shallow Patagonian Shelf. Inclusion of data that give information on dive duration in relation to depth partially negates this problem, and shows quite clearly that imperial cormorants stand out in having a generally longer dive duration for any given depth than non-blue-eyed species (Fig. 5A). However, this performance in terms of duration is apparently mirrored by excessively long recovery periods at the surface following dives (Fig. 5B). Clearly, birds of the blue-eyed complex are different from other cormorants, and we speculate on why this is by discussing what is known about bird physiology and standard physics (see below).

Firstly, why do imperial cormorants take so long to recover from dives (Fig. 5B)? The surface recovery period is necessary for divers to acquire the oxygen lost during the dive (as well as to clear carbon dioxide), and if the recovery period is excessively long, the implication is that correspondingly larger amounts of oxygen have been used during the dive (Wilson & Quintana 2004); however, the excessive surface durations after exceptionally long dives may also be due to an increasing anaerobic component of the dive. Since oxygen use is considered a proxy for metabolic rate (Schmid et al. 1995, Schmidt-Nielsen 1997, Enstipp et al. 2006), it might seem reasonable to suppose that imperial cormorants use more energy for their dives, at least in the duration range where they can be compared with other species. There are 4 major features that modulate metabolic rate in diving cormorants: water temperature (Enstipp et al. 2005, 2006), speed (Schmid et al. 1995, Lovvorn et al. 2004), the heat increment of feeding (Enstipp et al. 2005, 2006) and dive depth (Enstipp et al. 2006). The proportion of energy allocated to the heat increment of feeding is unlikely to differ among species because cormorants are primarily piscivores (Johnsgard 1993), and birds should be ingesting an approximately constant percentage of

their body mass and using a corresponding amount of energy to digest it.

The descent speed of cormorants is generally high (0.8 to 1.5 m s^{-1}) but constant, with no obvious difference between blue-eyed and other cormorants (Croxall et al. 1991, Watanuki et al. 1996, Kato et al. 2006, Watanuki et al. 2006). Superficially, at least, temperature does not appear to be important in accounting for the difference either, because the imperial cormorants we studied in Argentina were operating in water at temperatures similar to those experienced by other species documented in Fig. 5B (note that 3 species were diving in the same general area). We suggest, therefore, that the effects of depth are the primary driver for the observed differences between blue-eyed and other cormorants. Depth is important because depth-dependent pressure affects the volume of air in bird plumage (Lovvorn & Jones 1991), which in turn affects both the mechanical work required to overcome buoyancy (Lovvorn & Jones 1991, Lovvorn 1999, 2001) and heat loss (Gremillet et al. 1998b, Enstipp et al. 2006). Indeed, in a recent study, Wilson et al. (2006) noted how overall dynamic body acceleration (ODBA) in great cormorants (as measured by animal-attached accelerometers) correlated closely (r^2 = 0.81) with rate of oxygen use, and how ODBA in free-living imperial cormorants correlated extremely well (r^2 = 0.97) with calculated relative buoyancy.

Effect of plumage air on dive energetics

The general effect of plumage air on the energetics of diving in cormorants can be simplified by considering the power output required to take bodies with associated air to specific depths. We propose to ignore drag effects because descent speed did not change with depth, and suggest that the conversion by birds of aerobic power input into mechanical power output can be assumed to be roughly constant (Schmidt-Nielsen 1997). Thus, the upthrust (U, in Newtons) at any given depth is:

$$U = g\left(V\{1/[1+(D/10.3)]\}\right)$$

where V is the volume of air at the surface, D is depth (m) and g is the gravitational constant. The power (P, in Watts) required to overcome the upthrust and to move the body down the water column is simply given by the rate of change of depth ($\Delta D/dt$) of the volume so that:

$$P = U(\Delta D/dt)$$

Applying this to hypothetical imperial cormorants with a mass of 2 kg and body density (excluding air) of 1.03 g ml^{-1} (Wilson et al. 1992) with, and without, a substantial amount of plumage air (90 vs. 300 ml kg^{-1}; values representing the minimum documented for cormorants and a value for other divers such as auks or diving ducks [Wilson et al. 1992, Gremillet et al. 2005b]
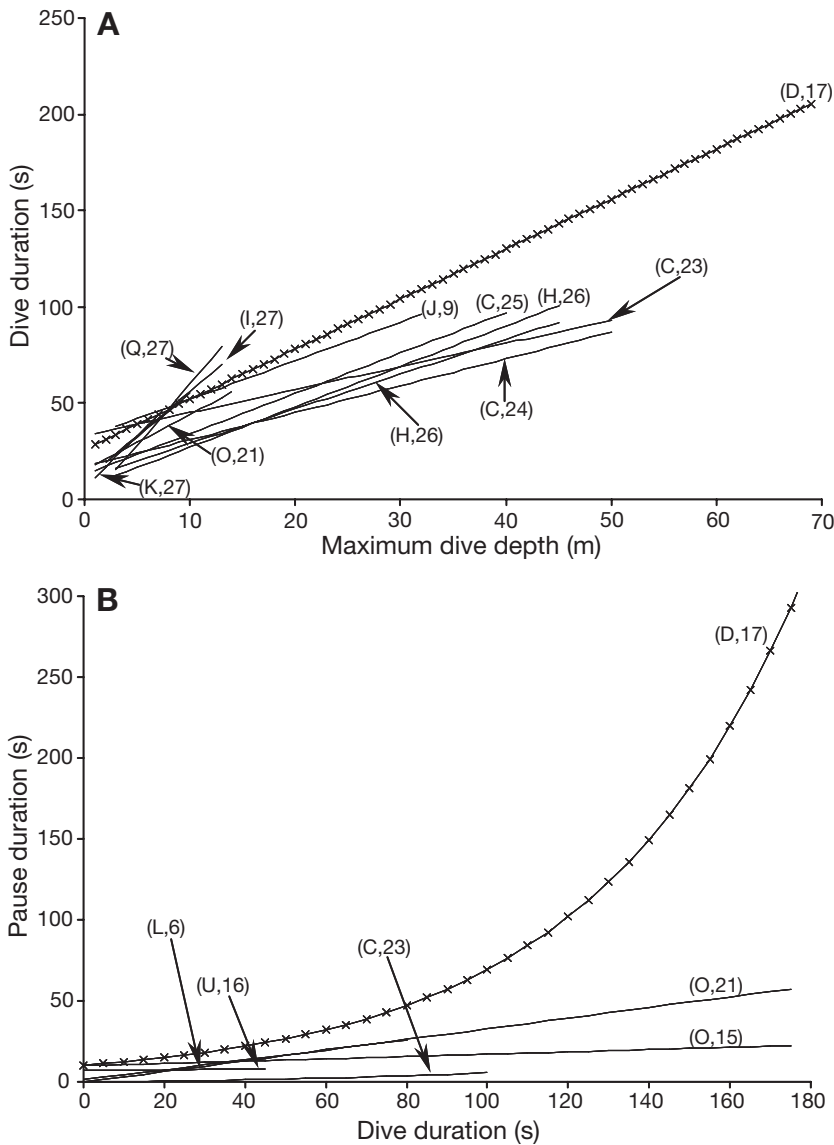

Fig. 5. Relationships between (A) dive duration and depth and (B) inter-dive (pause) duration and duration of previous dive for various species of cormorants. Lines refer to best-fit regressions presented in the literature and run from min. and max. values given in the source. For ease of identification, our data from *Phalacrocorax atriceps* (the only blue-eyed species) are shown as —×—. Letters and numbers refer to species and source (see Fig. 4)

descending the water column at an approximate rate of 1.5 m s^{-1} [see above]) indicates that the volume of air contained in the plumage makes a huge difference to mechanical power required for the descent (Fig. 6A). The instantaneous power requirements can be integrated to determine the cumulative mechanical energy needed to take these 2 hypothetical birds down the water column (Fig. 6B), and the division of this energy at any depth by the time taken to reach it can be used to determine the mean mechanical power output necessary for the descent. Again, the difference between the hypothetical bird with much and little air is sub-stantial, differing by a factor of about 3. This highlights the importance of plumage air volume in modulating the diving energetics, and is borne out by field and captive studies on diving birds for both the descent and bottom phase of the dive (Sato et al. 2002, Lovvorn et al. 2004, Tremblay et al. 2005, Watanuki et al. 2005, 2006, Enstipp et al. 2006, Kato et al. 2006). Thus, a difference in plumage air volume may well account for the differences we observe between imperial and other cormorants not of the blue-eyed group. This effect may be further modulated by variation in the amount of air inhaled prior to diving; it has been noted that some diving birds inhale more when diving deeper (Sato et al. 2002, Wilson & Zimmer 2004) because respiratory volume-mediated upthrust decreases with depth. Thus, deep-diving birds may use more energy to descend; however, it is predicted that the extra oxygen provided by respiratory spaces at the final foraging depth and the passive ascent from a greater depth compensate for this (Wilson & Zimmer 2004).

The law of heat conduction states that the rate of heat loss is inversely proportional to the thickness of insulation. In the case of cormorants, heat loss to the water—another major factor modulating metabolic rate (Enstipp et al. 2005, 2006)—will vary linearly with plumage thickness (and therefore volume). Thus, a simplified representation of the benefits and costs to cormorants of swimming along the sea bed at various depths with 2 different amounts of air in their plumage (much air: e.g. 300 ml kg^{-1}, and little air: e.g. 90 ml kg^{-1}) can be constructed by considering that birds generate a fixed proportion of heat as a result of muscular activity (Schmidt-Nielsen 1997) and that this activity is directly related to upthrust (Fig. 7). This assumes that bird body temperature remains constant (cf. Wilson & Gremillet 1996, Enstipp et al. 2005). Heat loss from the bird will be determined by the thickness of the plumage (inversely proportional to plumage volume), which varies with depth (Gremillet et al. 1998b) (Fig. 7). If the cormorant swimming along the sea bed is to maintain thermal homeostasis with no cost other than that involved in locomotion, then the heat generated from the effort involved in swimming must always exceed that lost (bird with much plumage air in Fig. 7 up to depths of at least 70 m). At depths where
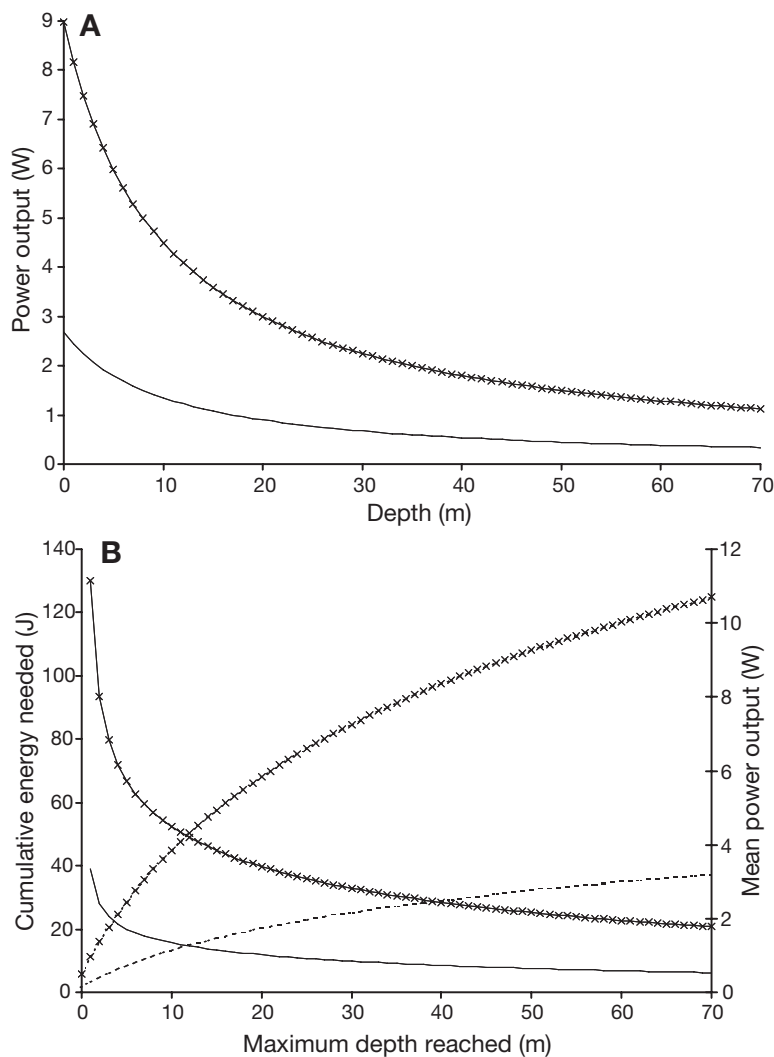

Fig. 6. (A) Instantaneous mechanical power required to descend 2 cormorant bodies, identical in physical characteristics (mass = 2 kg, density 1.03 g ml^{-1}) except for volume of associated air (—✗— = 300 ml kg^{-1}, ——— = 90 ml kg^{-1}), down the water column at a rate of 1.5 m s^{-1} as a function of depth. Note that this does not take into account forces due to drag. (B) Cumulative mechanical energy needed to take the 2 cormorant bodies shown in (A) to a specific depth (rising curves: —✗—, bird with 300 ml air kg^{-1}; -------, bird with 90 ml air kg^{-1}) and mean power output needed to achieve this (descending curves: —✗—, bird with 300 ml air kg^{-1}; ———, bird with 90 ml air kg^{-1})

heat loss exceeds that produced during locomotion, the bird must increase energy expenditure to compensate.

Our model (which is mechanistic, does not incorporate behavioural or physiological complexities that might help regulate heat loss, and instead uses representative values from birds and is intended to show trends rather than absolute values) shows that the energy expended for swimming along the bottom is less for the bird with little plumage air at depths between 0 and 40 m, but less for the bird with much plumage air at deeper depths than this (Fig. 7). This indicates how different plumage characteristics may allow birds competitive advantages at different depths. Substantially increasing energy expenditures in cormorants with little plumage air beyond their critical depth (where heat loss exceeds that generated) would imply that inter-dive surface pauses should increase in an accelerating fashion unless, during such deep dives, body temperature falls. Such decreases in body temperature have been observed in at least some cormorant species (Wilson & Gremillet 1996) but do not seem to be the norm (Enstipp et al. 2005, Gremillet et al. 2005a). Ultimately, however, either substantial temperature drops during diving or excess heat loss at the surface during extended resting following prolonged

diving (when heat generation is minimized) (Enstipp et al. 2005) would be expected to shorten the period over which cormorants with little plumage air can actively remain at sea. This condition will be exacerbated by cold water.

We thus propose that differences in dive performance between cormorants of the blue-eyed taxon stem from differences in plumage air volume, with blue-eyed cormorants having substantially more air in the non-wettable part of the plumage (Gremillet et al. 2005b). There is certainly great interspecific variability in plumage air even among cormorants: for example, Wilson et al. (1992) noted that cape cormorants *Phalacrocorax capensis* have 3 times as much plumage air per kg body mass as great cormorants *P. carbo*. Additional support for this proposition derives from 2 other pieces of evidence. Firstly, the stroke frequency of the imperial cormorant descending the water column at a rate of 1.5 m s^{-1} (Fig. 3) was consistently higher than that of similarly sized great cormorants descending the water column at the same rate for any depth (values are ca. 4.5 vs. 3.1 Hz at 5 m, 3.3 vs. 2.8 Hz at 10 m and 2.2 vs. 2.1 Hz at 20 m for imperial and great cormorants, respectively; see Kato et al. 2006). However, values were similar to those recorded for the European
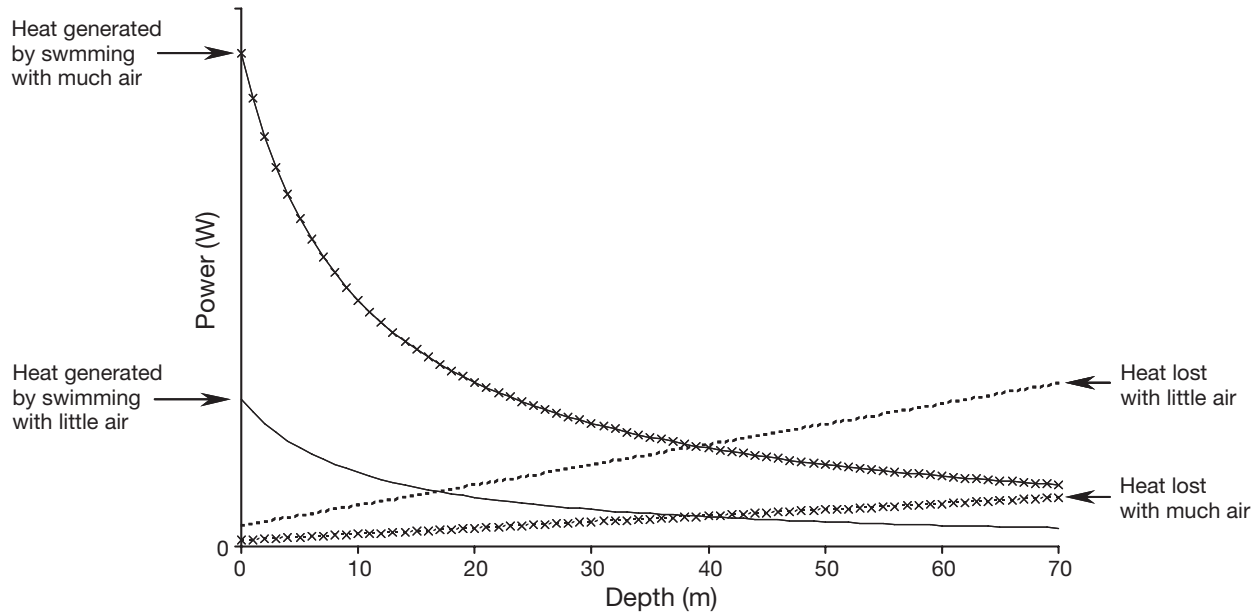

Fig. 7. Heat generation and loss based on mechanical power of 2 cormorants, identical except for amount of air contained in the plumage (much vs. little air), swimming at the sea bed at different depths. Mechanical power calculated assuming that it is linearly related to upthrust, which is itself inversely related to depth (see equation in text). Heat generated by the cormorant with much plumage air (assumed to comprise 70% of energy used per second) is greater than that of bird with little plumage air over all depths (due to greater power required to counter upthrust); heat loss is also less in the cormorant with much plumage air (following the law of heat conduction, where energy loss is proportional to temperature difference and inversely proportional to the insulating layer). In this scenario, heat lost by the bird with much plumage air never exceeds that generated. The bird with little plumage air loses more heat than it generates at 16 m, and so must generate extra heat to compensate if body temperature is not to drop. At 40 m and deeper, energy expended by the bird with little plumage air exceeds that of the bird with much plumage air

shag (Watanuki et al. 2005), a cormorant that also regularly dives to remarkable depths (Wanless et al. 1999). Secondly, although they may forage in water at temperatures close to 0°C (Johnsgard 1993), cormorants from the blue-eyed group spend extended periods at sea (e.g. means of between 150 min [our data] and 210 min [Kato et al. 1992] for *P. atriceps*, ca. 120 min for *P. albiventer* [Kato et al. 2000] and 194 min for *P. nivalis* [Green & Williams 1997], and up to a maximum of 390 min [our data]). This contrasts starkly with some other cormorants, notably *P. carbo*, which is known to contain very little plumage air (170 ml kg^{-1}) (Gremillet et al. 2005b) and is limited to a mean daily foraging time of just 9 min in water at –2°C (but will forage for a daily mean of about 45 min at 8°C and 150 min at 13°C) (Gremillet et al. 2001, but see Gremillet et al. 2005a). We note again that European shags (which do not belong to the blue-eyed complex) appear atypical, and may spend up to 7 h d^{-1} in northern European waters at temperatures around 9°C (Daunt et al. 2006).

Our proposition could be substantiated by determining the volume of air in the plumage of cormorants of this group and examining the feathers according to methods detailed by Gremillet et al. (2005b). However, in order to obtain a reasonable sample size, this approach requires that birds be specifically killed for this purpose, which we felt was not ethically justified.

Our treatise purports that imperial cormorants, together with other members of the blue-eyed group, have plumage that is atypical of cormorants in that it contains substantial amounts of air. It may be that the distribution of blue-eyed cormorants, being limited to the colder waters south of 43° (Johnsgard 1993), gives these birds a competitive advantage over other cormorants as a result of their better insulation. However, we would expect this advantage to be eroded as water temperatures increase, to instead favour other cormorant species. In higher water temperatures, blue-eyed cormorants could maintain a competitive advantage over other species by diving deeper (and therefore longer) because deep dives expose birds to thermally more stressful environments. In this regard, it is notable that mean dive durations of imperial cormorants studied here (100.4 s) were markedly longer than those reported for rock shags *Phalacrocorax magellanicus* (47 s) (Quintana 1999), red-legged cormorants *P. gaimardi*) (26.8 s) (Frere et al. 2002) and neotropic cormorants *P. olivaceus* (19 s) (Quintana et al. 2004), and that mean maximum depth of birds in this study was between 40 and 115% greater than those suggested for rock shags (Quintana 1999), red-legged cormorants (Frere et al. 2002) and neotropic cormorants (Quintana et al. 2004), all of which breed sympatrically with imperial cormorants along the Patagonian coast of Argentina (Frere et al. 2005). However, deep diving must be balanced by appropriate prey densities to make the increased transit time between the surface and bottom profitable. Future studies could address the rates of prey acquisition in cormorants in general (Gremillet et al. 2001, 2004), and in blue-eyed cormorants in particular, in order to determine how prey density with depth equates with appropriate dive strategies and net energetic gain after taking into account the factors that modulate metabolic rate. Other than that, a global examination of the depths and temperatures exploited by various cormorant species in relation to plumage air volume (perhaps facilitated by the simple methods proposed by Wilson et al. 1992) might go some way to help explain patterns of distribution in these remarkable birds.

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